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The effects of seagrass patch size and energy regime on growth of a suspension-feeding bivalve

by E. A. Irlandi[1,2]

ABSTRACT

An investigation of how the presence of seagrass and seagrass patch size in high- and low-energy environments affected growth of an infaunal bivalve (hard clam, *Mercenaria mercenaria*) was carried out. Two general size classes of clams were used, mean length ca. 40.0 mm (41.9 mm) and mean length ca. 20.0 mm (22.3 mm and 19.0 mm), to see if growth responses were the same for large- and small-sized clams. Seagrass density, length and species composition as well as sediment characteristics were measured at high- and low-energy sites to determine if changes in seagrass and/or sediment dynamics could explain observed growth patterns. The incidence of siphon cropping was also evaluated as a potential influence on clam growth. Large clams grew faster inside than outside vegetation at both high- and low-energy sites. Within the vegetation, growth of large clams was faster in medium-sized patches of seagrass (2–3 m across) than in small patches (1 m across) and was intermediate in large patches (> 4–5 m across). There was no apparent correlation between seagrass shoot density, blade length, or species composition and growth of clams in patches of different size. Growth of small clams (22.3 mm) within seagrass was independent of the two seagrass patch sizes tested (large vs. small), but did vary among sites. Growth of clams was not correlated with differences in shoot density, blade length or species composition among sites. Growth of small clams (19.0 mm) also varied with energy regime and with presence/absence of vegetation. Small clams grew significantly more within seagrass under both high- and low-energy conditions, but the effect was more pronounced at high-energy sites than at low. Seagrass shoot density, blade length, and species composition did not vary between high and low energy regimes, but did vary among sites from the beginning to the end of the experiment. Long-term averages of sediment stability based on grain size characteristics suggest that the baffling effect of seagrass varies greatly with energy regime. Vegetated sediments at high-energy sites contained significantly more fine material than the unvegetated sediments while there was no difference in the fine fraction between vegetated and unvegetated sediments at low-energy sites. The difference in sediment stability between seagrass cover under high- and low-energy conditions may contribute to the magnitude of the difference in the growth response of small clams to the presence of vegetation at exposed and protected sites. Other factors also contributed to the increased growth of clams in seagrass beds at the protected sites where grain size analysis suggests similar sedimentary dynamics both within and outside of the

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vegetation. Mean adjusted siphon weights, however, for both large and small clams were independent of seagrass cover and energy regime implying that siphon nipping differences did not influence growth patterns of clams. Based on this study, and previous investigations, the effect of seagrass cover on growth of clams appears to be the result of a complex interaction among food supply, predation disturbance, and sediment stability with the relative importance of these processes varying with size of the clam, hydrographic regime, and local site differences.

1. Introduction

Benthic suspension feeders depend on water flow to supply them with food. If the overlying water is not replaced quickly enough, local depletion of edible particles can occur in near-bottom waters (Glynn, 1973; Buss and Jackson, 1981; Peterson and Black, 1987, 1991). Rapid current flow reduces local food depletion by increasing flux of food particles both through horizontal advection and also through enhanced vertical mixing of the water column (Wildish, 1977; Wildish and Kristmanson, 1979, 1985; Fréchette *et al.,* 1989; Monismith *et al.,* 1990). Because of this relationship between food delivery and flow, most suspension feeders grow rapidly where flow speeds are fast, up to a point where excessive flows may inhibit feeding activity (Wildish and Kristmanson, 1979; Wildish *et al.,* 1987). Growth of the hard clam, *Mercenaria mercenaria* L., in unvegetated sediments has been shown to be greater in fast flows than in slow flows (Grizzle and Morin, 1989; Grizzle *et al.,* 1992).

Hard clams, however, also occur in vegetated sediments where seagrass shoots and leaves projecting into the water column reduce current flow (Ginsburg and Lowenstam, 1958; Fonseca *et al.,* 1982; Peterson *et al.,* 1984; Gambi *et al.,* 1990). Based on hydrodynamics alone, one would predict decreased growth of clams within the reduced current velocities inside a seagrass bed. Studies comparing hard clam growth from vegetated and unvegetated sediments, however, have demonstrated all possible outcomes; increased, decreased and no effect on growth (Kerswill, 1949; Peterson *et al.,* 1984; Peterson and Beal, 1989; Arnold *et al.,* 1991; Coen and Heck, 1991; Irlandi and Peterson, 1991; Beal, 1994). Several possible explanations, including food availability (Peterson *et al.,* 1984; Irlandi and Peterson, 1991; Judge *et al.,* 1993), disturbance by predators (Irlandi and Peterson, 1991), and siphon cropping (Coen and Heck, 1991; Irlandi and Peterson, 1991), have been presented to explain why growth of hard clams does not always decline with the slow current velocities associated with seagrass habitats.

Physical, abiotic disturbances including sediment resuspension may also influence growth of clams. Suspension feeders often grow more slowly when exposed to high suspended sediment loads due to the energy expenditure required to process inorganic particles in order to obtain their food (Bricelj and Malouf, 1984; Bricelj *et al.,* 1984; Turner and Miller, 1991). Dynamic sedimentary environments may also demand an energetic cost to maintaining a feeding position within the sediments that may exceed the profits achieved during periods of successful feeding (Myers, 1977).

The root-rhizome mat of seagrass plants bind and stabilize sediments (Ginsburg and Lowenstam, 1958; Scoffin, 1970; Orth, 1977; Fonseca and Fisher, 1986). The seagrass blades also attenuate wind waves and reduce sediment transport and resuspension beneath the seagrass canopy (Ward *et al.*, 1984; Fonseca and Fisher, 1986; Fonseca and Cahalan, 1992). These changes in the sediment dynamics with the presence of aquatic vegetation may have profound effects on suspension-feeder growth and may explain why some investigations have demonstrated increased growth within seagrass beds while others have not.

Previous studies comparing clam growth with and without seagrass cover in North Carolina suggest that the hydrodynamic setting of the seagrass bed may determine what effect the vegetation has on growth of clams. Peterson and Beal (1989) found slow growth rates for clams in unvegetated sediments at their highest-energy site (based on sediment grain size) and the effect was more pronounced for small-sized clams (ca. 30 mm shell length) than for large (ca. 60 mm shell length). They argued that smaller clams are less massive, burrow less deeply, and have shorter siphons, all implying greater sensitivity to surface sedimentary disturbances. Irlandi and Peterson (1991) also saw a strong reduction in growth of small-sized clams (< 30 mm shell length) in the absence of seagrass cover at a high-energy exposed site. When they experimentally reduced the length of the seagrass blades allowing waves to penetrate the canopy and impinge on the seafloor, growth of clams was reduced compared to growth from seagrass beds with intact canopies. Both of these studies suggest that sediment stability by seagrasses, particularly at high-energy sites, may contribute to differential growth patterns of hard clams from vegetated and unvegetated sediments.

The objective of this study was to examine the effects of seagrass cover and seagrass patch size at replicate high-energy exposed sites and replicate low-energy protected sites on growth of two size classes of clams (large-ca. 40 mm and small-ca. 20 mm in shell height). The effect of seagrass patch size has not been previously investigated, and it is reasonable to predict that small patches of vegetation may not modify the flow regime and sediment dynamics the same as large patches of vegetation. The roles of sediment stability, seagrass characteristics (density, length, and species composition), and predation disturbance (lethal-see Irlandi, 1993 and sub-lethal) in controlling growth of clams among treatments were examined.

2. Materials and methods

a. Study sites. Two high-energy exposed sites and two low-energy protected sites in Back Sound, North Carolina, USA were chosen (Fig. 1). Cape Lookout (CL) and Oscar Shoal (OS) were representative of high-energy conditions and Bottle Run Point (BP) and Middle Marsh (MM) were representative of low-energy conditions. Initial energy classifications were based on gross sediment characteristics, qualitative observations of ambient current flow, and degree of exposure to wind-generated

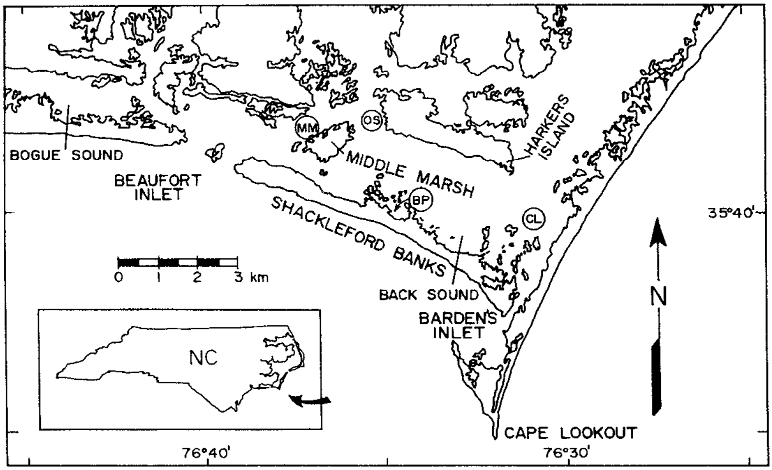

Figure 1. Location of study sites in Back Sound, NC, USA. MM = Middle Marsh, BP = Bottle Run Point, OS = Oscar Shoal, and CL = Cape Lookout.

waves. Sediment cores, chalk block dissolutions, and current velocity readings were taken at each of the four sites to confirm the classifications of high- or low-energy (see below). Water depth at the four sites ranged from about 10–40 cm at low tide to 120–150 cm at high tide. Most seagrass beds used in the experiments were mixtures of *Halodule wrightii* and *Zostera marina.* In North Carolina, these two species of seagrass vary in their abundance both seasonally and among sites. It is difficult to do long-term experiments in which one can adequately control for variation in shoot density, blade length, and/or species composition of the grass. Therefore, seagrass characteristics (density, blade height, and species composition) were measured at the beginning and end of all experiments to determine if changes in these variables with patch size and energy regime were correlated to growth of clams (see below for detail on sampling methodology).

b. Energy characterization. Sediment composition can be an indirect measure of energy regime with coarse, sandy sediments indicative of high fluid energy and fine sediments with high organic content indicative of low fluid energy (see Fonseca *et al.,* 1982; Bell *et al.,* 1994). To determine the sediment composition at each of the four sites, four replicate surface cores (4.7-cm diameter by 3-cm deep) were taken in the fall of 1990 from the unvegetated sediments. Cores were analyzed for %fines and %sands using standard wet sieving techniques (Folk, 1974), and %combustible organic content was determined by heating samples at 500°C for 12 hours in a muffle furnace. Since the fine and sand fractions are related to each other (sums totaling 100%) only the arcsine-transformed proportion of the fine fraction and the organic content were analyzed as the dependent variables in separate one-way ANOVAs with site as the independent variable. Prior to analyses, all cell means in this and all subsequent experiments were tested for homoscedasticity of error variances with an $F_{\max}$ test ($\alpha = 0.05$).

To obtain an integrated measure of water motion from currents and waves, the dissolution of carpenter's chalk blocks on several days encompassing a range of wind conditions was measured (Doty, 1971; Santschi *et al.,* 1983). Pre-formed hemispheres of carpenter's chalk (basal diameter 5.5 cm, height 3 cm) were dried at 60°C for 24 hours and weighed to the nearest 0.01 g. Ten to 20 chalks were placed individually in small (8 cm × 8 cm × 6 cm) vexar cages (6-mm mesh) that were anchored to the seafloor with 15-cm wire staples. Chalks were left in the field for 48 hours, retrieved, rinsed in fresh water, and oven dried at 60°C to a constant weight (0.01 g). To control for weight-loss in still water and weight-loss changes with water temperature, six chalk blocks were placed in individual 5-gallon buckets with sea water pumped from Bogue Sound and held in the laboratory during each 48-hour run. The water in the buckets was changed after 24 hours to reduce saturation. The mean weight-loss in still water for each 48-hour period was subtracted from the weight-loss of each block placed in the field to obtain a corrected weight-loss. Separate one-way ANOVAs were performed on the corrected weight-loss for each run with site as the independent variable. $F_{\max}$ tests ($\alpha = 0.05$) on the cell means indicated heteroscedastic error variances for all runs, except #5. Data from all other runs were log-transformed to homogenize variances prior to analyses.

Current velocities at the four sites were measured with Marsh McBirney Model 201-D electromagnetic current meters. On 8 July 1991 four replicate free-stream (maximal flows not impeded by bottom-associated drag) current velocity readings (averaged over a 30 s time interval) were taken every 20 minutes over a six-hour incoming tidal period at each of the four sites simultaneously. The depth in the water column that the readings were taken varied from site to site but was approximately 0.5 m from the seafloor. The heights of 12 passing waves were also recorded at the 20-minute intervals by measuring the difference in water depth as a wave passed. Mean current velocities and wave heights were plotted over time for each site to allow visual comparisons.

c. *Growth of large clams—Seagrass patch size and energy effects.* Metal posts were used to mark the corners of four replicate 75 cm × 75 cm plots in unvegetated sediments and in small (1 m across), medium (2–3 m across), and large (4–5 m up to 15–20 m across) seagrass patches at each of the four sites. These dimensions are representative of the range of patch sizes available in nature at both high- and low-energy sites (personal observation). One 15-cm deep by 9.8-cm diameter core from each seagrass patch was used to characterize the vegetation for the different patch sizes at each site at the beginning (August 1990) and end (December 1990) of the experiment. From these cores, the number of shoots for each species of seagrass was counted (*Halodule wrightii* and *Zostera marina*) to determine density of shoots per m^2 and species composition, and the mean of the longest blade per shoot was recorded. Separate four-factor ANOVAs with date (fixed), energy regime (fixed), site (nested within energy regime-random), and patch size (fixed) as the independent variables were used to examine variation in mean blade length, mean shoot density, and % *Zostera* (arcsine transformed) among treatments.

Buried vexar fences constructed from 75-cm long by 10-cm high strips of 6-mm unoriented vexar mesh with 75-cm long corner posts enclosed the sand plots. The subsurface enclosures were intended to reduce emigration of clams from the unvegetated treatments without obstructing flow. Very little scouring of sediments occurred around the enclosures. When scouring did occur, the enclosure walls were reburied. Enclosures have been shown to be effective in retaining infaunal bivalves (Peterson and Black, 1993) and have been used successfully in other studies with hard clams (Peterson, 1982; Peterson and Beal, 1989). Because the root-rhizome mat within the seagrass naturally inhibits clam migration, and installation of enclosure walls would destroy the vegetation, enclosures were not used in the seagrass treatments.

In August 1990 32 clams (all clams used in this and subsequent experiments were obtained from a hatchery to ensure similar genetic stock) with a mean length of 41.9 mm (± 0.96 SE, $n = 2048$) were individually marked with Mark Tex Corp. inks, measured with vernier calipers to the nearest 0.1 mm from anterior to posterior end, and placed in living position in each of the experimental plots (density = $57/m^2$). A relatively narrow size range of animals was used in this and all subsequent experiments to avoid any influence of initial size on growth of clams. Natural densities for hard clams in this region range from $1.6/m^2$ in unvegetated sediments to $9/m^2$ in vegetated sediments (Peterson *et al.,* 1984). High densities were used to ensure that enough animals would be recovered at the end of the experiment to obtain accurate estimates of growth. Previous studies in North Carolina waters also indicate that reduction of growth is minimal (ca. 14%) at densities of up to 80 clams/m^2 (Peterson and Beal, 1989). In late November/early December 1990 all plots were dug by hand to recover marked live and dead clams. All live clams were identified to individual and remeasured. Separate three-factor ANOVAs with energy (fixed), site (nested within energy regime-random), and patch size (fixed) were used as the independent variables to confirm that the mean initial size of all surviving clams within each plot were similar across all treatments and to see if the mean growth of clams within each plot varied among treatments.

Loss of siphon tissue due to browsing, may affect bivalve growth (Peterson and Quammen, 1982; Coen and Heck, 1991; Irlandi and Peterson, 1991; Kamermans and Huitema, 1994). When hard clams are caged with siphon-nipping fishes, siphon weights adjusted for body weights are lighter than for clams caged without fish (Irlandi and Mehlich, 1995) indicating that the fish remove siphon tissue. Mean siphon weights of clams used in the experiment were compared to determine if patterns in siphon weights, as an indicator of siphon nipping disturbance, matched patterns in growth. A subset of five clams that were recovered live from each plot at the end of the experiment was sacrificed (heat killed) and the fused inhalant and exhalant siphons were dissected from the body tissue. Siphon and body tissues were dried at 60°C until constant weight. A three-factor ANCOVA was used to compare differences in mean siphon weights from each plot, taking into account variation in mean body weights, with energy (fixed), site (nested within energy regime-random), and patch size (fixed) as the independent variables. Slopes of regression lines used in the ANCOVA were compared to ensure that they were parallel and error variances of the regression equations were determined to be homoscedastic prior to the analysis.

d. Growth of small clams—Seagrass patch size effects. In the Spring of 1991 the experiment was repeated using a smaller size class of clams (mean length 22.3 mm ± 0.02 SE, $n = 2880$) to see if growth patterns were similar for small and large clams. The design was as described above except medium-sized seagrass patches were not used. Attention was focused on the extremes in patch size (small vs. large), and replication was increased from $n = 4$ to $n = 6$ replicate plots for the remaining three treatments (unvegetated, small, and large patches) at each of the same four sites. Vegetation characteristics were determined using the methods stated above and 40 marked and measured clams were placed in living position in each plot in May 1991 (density = $71/m^2$). In August 1991 seagrass samples were taken again, and all plots were dug by hand to recover live and dead marked clams. Unfortunately, the grass at one of the high-energy sites (Cape Lookout) was nearly gone by the end of the experiment. This site was dropped from the analysis precluding a definitive comparison between high- and low-energy environments on small clam growth. Also virtually no clams (only 8 of 1380) were recovered live from the unvegetated plots due to high rates of predation. Therefore, separate two-way fixed-factor ANOVAs with site and patch size (small vs. large) were used as the independent variables to confirm that the mean initial sizes of all surviving clams within each plot were similar across all treatments and to determine if the mean growth of clams differed among treatments. Separate three-way fixed-factor ANOVAs with date, site, and patch size as the independent variables were used to examine variation in seagrass blade length, shoot density, and species composition (*%Zostera*).

Comparisons of mean siphon weights among the different treatments were made using a two-factor ANCOVA with site (fixed) and patch size (fixed) as the independent variables. Slopes were determined to be parallel, and regression error variances homoscedastic prior to analysis. In addition, all clams that were recovered live were sacrificed, not just a subset of five.

e. Growth of small clams—Energy and grass cover effects. Growth experiments with small-sized clams (mean shell length 19.0 mm ± 0.10 SE, $n = 150$) using a different methodology to gain greater survivorship and replication from the unvegetated sediments were repeated. Since growth of small clams did not vary between large- and small-sized patches in the previous experiment (see results below), patch size as a factor was omitted and only vegetated and unvegetated treatments at three high- and three low-energy sites were used. The additional high-energy site was adjacent to the previously described Oscar Shoal site, and the additional low-energy site was located within the Middle Marsh complex. Seagrass characteristics were determined from five replicate cores taken from within the seagrass at each site at the beginning and end of the experiment. Variation in blade length, shoot density, and species composition were examined using separate three-factor ANOVAs with date (fixed), energy (fixed), and site (nested within energy-random) as the independent variables.

Rather than placing clams in replicate plots at unnaturally high densities, individual clams were placed at 1-m intervals along marked lines that were stretched between reference poles in and out of seagrass at the six sites. This removed the concern that predators may key-in on dense patches of prey and inflict high rates of mortality (e.g., Boulding and Hay, 1984; Sponaugle and Lawton, 1990; Mansour and Lipcius, 1991). This type of design also necessitated tethering of the clams to prevent emigration, especially in the unvegetated sediments. Clams were tethered to buried 15-cm wire staples by gluing one end of a 15-cm long piece of monofilament line to one valve of the clam and tying the other end to the staple. Before deployment in the field, clams were marked and measured as before. Clams were placed in the field by inserting the staple into the seafloor and then placing the clam in living position approximately 7 cm from the staple. 100 clams were placed in the vegetated and in the unvegetated sediments at each of the 6 sites in March and recovered in June 1992. A three-factor blocked ANOVA with site (nested within energy-random), energy (fixed), and seagrass treatment (fixed and blocked by site) was used as the independent variables to confirm that the mean initial size of all surviving clams were similar across treatments and to see if the mean growth of clams differed from the vegetated and unvegetated treatments at both high and low energy.

Mean siphon weights of all survivors were also compared among the different treatments as described above using a three-factor ANCOVA with site (nested within energy-random), energy (fixed), and seagrass treatment (fixed and blocked by site) as the independent variables.

f. Sediment stability—Energy and grass cover effects. To determine if seagrasses differentially stabilize sediments under high- or low-energy conditions, comparisons of the fine fraction were made from surface sediments collected in the fall of 1990 from vegetated and unvegetated sediments at the two high- and two low-energy sites. Four replicate surface sediment cores (4.7-cm diameter by 3-cm deep) were taken

Table 1. Mean percentages and results from separate one-way ANOVAs with site as the independent variable performed on arcsine-transformed proportions of fine material and organic content from four replicate surface sediment cores taken from unvegetated sediments at each of the four sites. Like superscript letters denote the sites that did not differ from each other in the Tukey *post hoc* tests following each one-way ANOVA. Numbers in parentheses represent ± one standard error. $F = F$ ratio and $P = P$ value from the ANOVAs.

Energy	Site	%Fines	Energy means	%Organics	Energy means
Low	Bottle Run Point	87 (0.9)^a	88 (1.1)	2.7 (0.3)^a	2.5 (0.2)
	Middle Marsh	89 (2.2)^a		2.2 (0.3)^a	
High	Cape Lookout	58 (2.0)^b	61 (1.7)	0.9 (0.1)^b	0.9 (0.2)
	Oscar Shoal	63 (2.4)^b		0.9 (0.3)^b	
		$F_{(3,12)} = 63.8; P < 0.01$		$F_{(3,12)} = 12.4; P < 0.01$	

from inside the seagrass beds and wet sieved to determine the composition of fines and sands (Folk, 1974). These samples were taken at the same time as those from outside the seagrass bed (as described above under *Energy characterization*) to allow comparisons of sediment grain size from vegetated and unvegetated sediments at high- and low-energy sites. Sediment samples were pooled across the two sites in each energy category and a two-factor fixed ANOVA with energy and seagrass treatment as the independent variables was used to analyze the arcsine-transformed proportion of fine material.

3. Results

a. Energy characterization. Although the sediment data and chalk dissolutions were descriptive measures of site characteristics and not a result of direct hypothesis testing, the ANOVAs were used to demonstrate statistical differences between high- and low-energy sites. The proportion of fines and organic content from sediment cores both indicated significant differences among sites confirming initial site selections as high or low energy (Table 1). The amount of fine material was about 40% greater at the low-energy sites than at the high-energy sites (88% ± 1.1 SE vs. 61% ± 1.7 SE, respectively; Table 1). The organic content of the sediments was also greater at the low-energy sites (by a factor of almost three) than at the high-energy sites (2.5% ± 0.2 SE vs. 0.9 ± 0.2 SE, respectively; Table 1).

Chalk block dissolutions performed on seven separate dates covering a range of wind conditions provided an integrated picture of water motion from currents and waves at each of the four sites. ANOVA results indicated significant differences in corrected weight-loss of dissolution blocks among sites on all dates (Table 2). In five of the seven trials, Tukey *post hoc* comparisons demonstrated greater weight-loss of chalks at the two high-energy sites (Oscar Shoal and Cape Lookout) than at the two low-energy sites (Bottle Run Point and Middle Marsh) (Table 2). Cape Lookout

Table 2. Mean corrected weight-loss (in grams) and results from separate one-way ANOVAs with site as the independent variable from chalk block dissolutions made on seven separate runs. Data were log-transformed for analysis on all runs except #5. Sites that did not differ significantly from each other in Tukey *post hoc* comparisons are denoted by like superscript letters. BP = Bottle Run Point, MM = Middle Marsh, CL = Cape Lookout, OS = Oscar Shoal. Numbers in parentheses represent ± one standard error. $F = F$ ratio and $P = P$ values from ANOVA.

Pun #	Energy	Site	Weight loss	Run #	Energy	Site	Weight loss
1	Low	BP	2.66 (0.85)^{b}	5	Low	BP	4.16 (0.37)^{b}
		MM	0.57 (0.26)^{c}			MM	3.09 (0.34)^{b}
	High	CL	10.46 (1.62)^{a}		High	CL	12.24 (0.57)^{a}
		OS	6.69 (0.84)^{a}			OS	11.25 (0.52)^{a}
	$F_{(3,33)} = 27.5; P < 0.01$				$F_{(3,56)} = 105.6; P < 0.01$		
2	Low	BP	2.10 (0.30)^{b}	6	Low	BP	8.80 (0.74)^{b}
		MM	1.27 (0.21)^{c}			MM	3.29 (0.53)^{c}
	High	CL	12.07 (0.63)^{a}		High	CL	14.57 (0.37)^{a}
		OS	3.37 (0.63)^{bc}			OS	13.56 (0.52)^{a}
	$F_{(3,36)} = 26.5; P < 0.01$				$F_{(3,49)} = 58.5; P < 0.01$		
3	Low	BP	3.15 (0.38)^{b}	7	Low	BP	2.69 (0.69)^{b}
		MM	3.17 (0.28)^{b}			MM	1.93 (0.15)^{c}
	High	CL	11.77 (0.46)^{a}		High	CL	11.28 (0.55)^{a}
		OS	8.10 (0.82)^{a}			OS	9.38 (0.70)^{a}
	$F_{(3,55)} = 31.7; P < 0.01$				$F_{(3,53)} = 23.3; P < 0.01$		
4	Low	BP	6.22 (0.56)^{b}				
		MM	0.32 (0.25)^{c}				
	High	CL	14.25 (0.59)^{a}				
		OS	7.89 (0.63)^{b}				
	$F_{(3,50)} = 88.6; P < 0.01$						

consistently registered as the highest energy site with the greatest weight-loss of dissolution blocks in all trials, and Middle Marsh was consistently the lowest energy site with the least amount of weight-loss. On only two of the seven days (Runs 2 and 4) was there any overlap in weight-loss between high- and low-energy sites.

Recordings of incoming tidal flows made simultaneously at the four sites also confirmed the initial high- and low-energy site classifications (Fig. 2a). As the incoming flow became well established, current velocities increased rapidly at Oscar Shoal and Cape Lookout (high-energy sites) peaking at about 33 cm/s while velocities at Middle Marsh and Bottle Run Point (low-energy sites) remained slow and relatively stable at around 5 cm/s (Fig. 2a).

The mean wave heights from 12 passing waves recorded at all four sites every 20 minutes during an incoming tide are plotted in Figure 2b. The day these data were

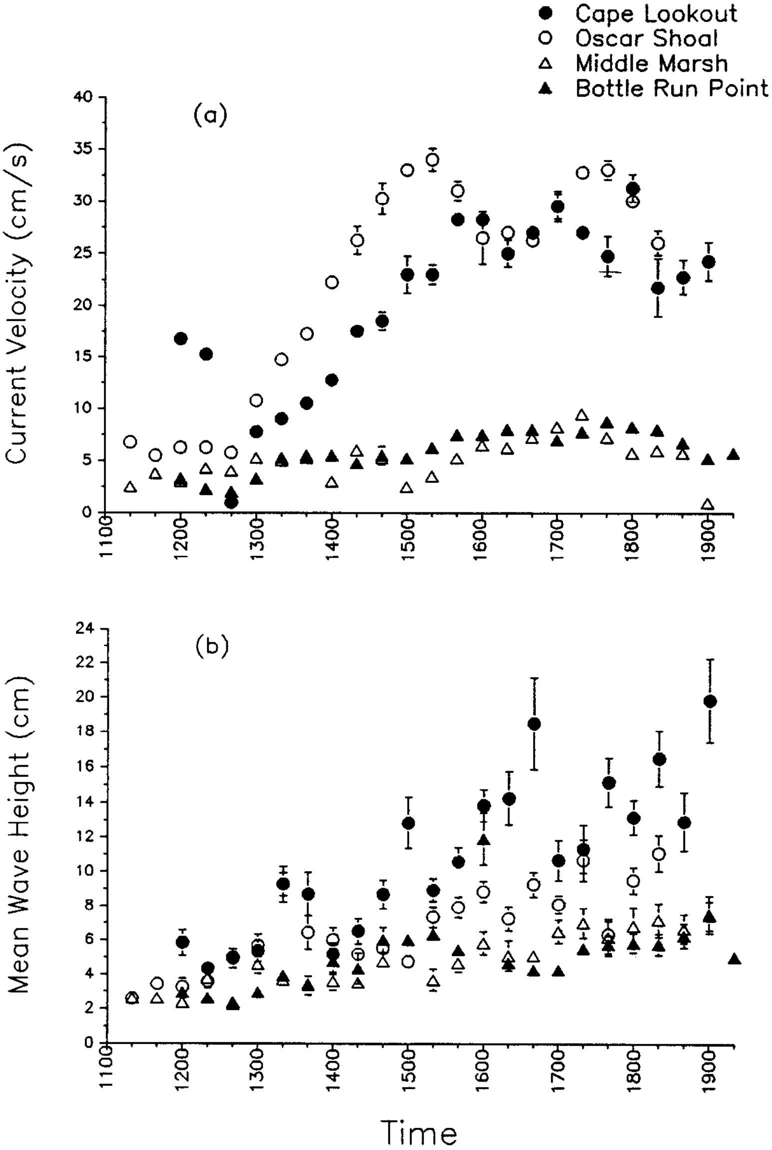

Figure 2. Plot of the mean from four replicate free-stream current velocity readings in cm/s (a) and mean wave heights (cm) from 12 passing waves (b) taken every 20 minutes for six hours at each site during an incoming tide. Error bars represent ± one standard error. Cape Lookout and Oscar Shoal represent high-energy sites, and Middle Marsh and Bottle Run Point represent low-energy sites.

collected was a "typical" summer day with a gentle (ca. 5 mph) southwest breeze building to a stronger breeze by late afternoon (ca. 10–15 mph). Winds peaked at 28 mph, with an average of about 12 mph for the day (H. Porter, unpublished data, UNC-Institute of Marine Sciences). Even on this relatively calm day the increase in wind speeds throughout the sampling period translated into a gradual increase in wave heights. Wave heights at all sites were roughly 4–5 cm during the first two hours of sampling. At the two high-energy sites the wave heights increased to about 14 cm while those at the two low-energy sites only increased to about 6 cm. The increase in variability about the means (i.e., larger error bars associated with the means) is also an indication of increased wave activity throughout the day. This is especially evident at the most exposed site, Cape Lookout.

b. Growth of large clams—Seagrass patch size and energy effects. ANOVA confirmed that the initial size of surviving clams did not differ among patch-size treatments, but did vary with site (Table 3a). Actual differences in the initial shell length among sites, however, were only 3–4 mm and most likely had little effect in producing growth patterns among sites. The ANOVA on growth of large-sized clams indicated a significant effect of site and seagrass patch size (Table 3b). In Tukey *post hoc* comparisons clams grew fastest in the medium- and large-sized patches, intermediate in the small-sized seagrass patches, and slowest in the unvegetated sediments (Fig. 3a). Growth was approximately 50–70% greater at Cape Lookout, Bottle Run Point, and Middle Marsh than at Oscar Shoal (Fig. 3b). No effect of seagrass patch size or energy regime was detected for siphon weights of clams, but there was a significant effect of body weight (the covariate) (Table 3c) and a marginally significant P value for the site by patch size interaction ($P = 0.06$).

Seagrass shoot density and %*Zostera* varied among sites and patch sizes (Table 4). Densities were lowest in small patches, intermediate from large patches, and greatest in medium patches while densities among sites varied by as much as a factor of 3.4 (Table 5a). There was a nonsignificant positive correlation between density of seagrass and growth of clams from the different patch size treatments (averaged over both dates— Pearson Correlation Coefficient = 0.93; $P = 0.24$) and a significant negative correlation between grass density and growth of clams among sites (averaged over both dates—Pearson Correlation Coefficient = -0.98; $P = 0.02$). Overall there was no significant relationship between density and growth when sites and patch sizes were combined in the correlation analysis (Pearson Correlation Coefficient = -0.53; $P = 0.22$). The amount of *Zostera* was greatest from large patches, intermediate in medium patches and lowest from small patches, and the seagrass beds at Cape Lookout had $<30\%$ *Zostera* while Middle Marsh was 100% *Zostera.* Growth of clams was not significantly correlated to the amount of *Zostera* present in the different patch sizes (averaged over both dates—Pearson Correlation Coefficient = 0.30; $P = 0.80$) or among the different sites (averaged over both dates—

Table 3. Results from the three-factor ANOVAs on (a) the mean initial size of surviving clams, (b) the mean growth of survivors, and (c) the mean siphon weights (ANCOVA with body weight as covariate) for large clams (mean size 41.9 mm) with energy (fixed), site (nested within energy regime-random), and patch size (fixed) as the independent variables DF = degrees of freedom, SS = sums of squares, $F = F$ ratio, $P = P$ value.

(a) dependent variable: mean initial size

Source	DF	SS	*F*	*P*
Energy	1	9.22	0.26	0.66
Site(Energy)	2	71.39	6.47	<0.01
Patch Size	3	4.75	0.23	0.87
Site(Energy)*Patch Size	6	40.65	1.23	0.31
Energy*Patch Size	3	10.96	0.54	0.67
Error	48	264.70		

(b) dependent variable: mean growth

Source	DF	SS	*F*	*P*
Energy	1	16.48	4.16	0.18
Site(energy)	2	7.92	4.05	0.02
Patch Size	3	45.21	11.26	<0.01
Site(Energy)*Patch Size	6	8.03	1.37	0.25
Energy*Patch Size	3	3.38	0.84	0.52
Error	48	46.92		

(c) dependent variable: mean siphon weight

Source	DF	SS × 10^{-2}	*F*	*P*
Energy	1	18.72	0.51	0.55
Site(Energy)	2	73.06	1.79	0.18
Patch Size	3	72.01	0.53	0.68
Site(Energy)*Patch Size	6	270.68	2.21	0.06
Energy*Patch Size	3	113.89	0.84	0.52
Mean Body Weight	1	366.72	17.96	<0.01
Error	47	959.77		

Pearson Correlation Coefficient = 0.83; $P = 0.17$). Shoot density and species composition did not vary from August to December samples, but blade lengths decreased significantly by 7 cm (Table 4, Table 5b). Blade lengths also varied among sites ranging from 12–13 cm at Bottle Run Point, Cape Lookout, and Oscar Shoal to 17 cm at Middle Marsh (Table 5b). There was no significant correlation between blade length and growth of clams among sites (averaged over both dates—Pearson Correlation Coefficient = 0.67; $P = 0.33$).

c. Growth of small clams—Seagrass patch size effects. ANOVA confirmed that the mean initial size of surviving clams did not vary among treatments (Table 6a).

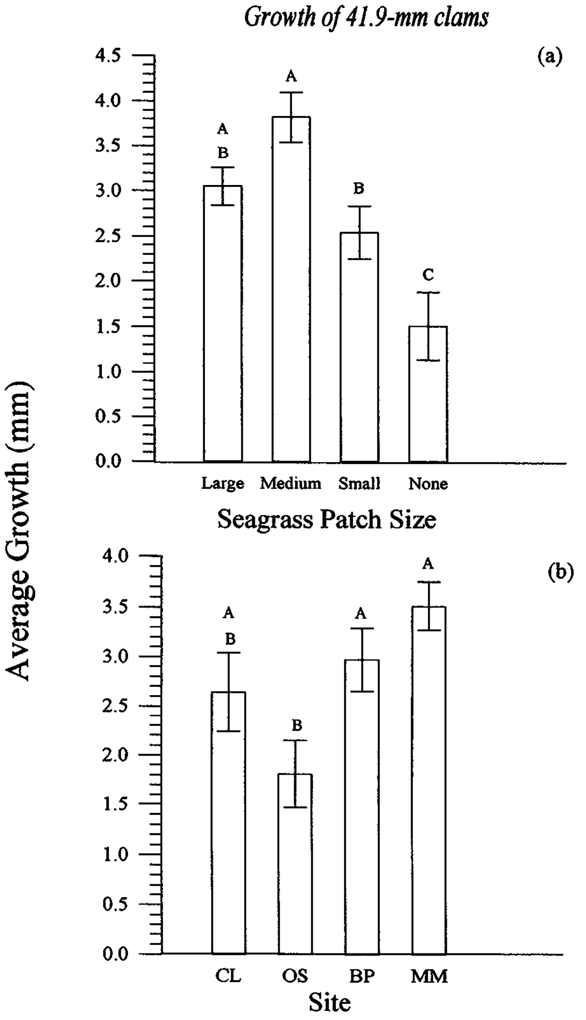

Figure 3. Average growth of large clams (41.9 mm) by seagrass patch size (a) and site (b). Error bars represent ± one standard error and like letters denote treatments that did not differ significantly from each other in Tukey *post hoc* comparisons. ANOVA results presented in Table 3b.

Growth of small-sized clams was independent of seagrass patch size but did vary among the three sites (Table 6b). Tukey *post hoc* comparisons indicated that growth at the Oscar Shoal site (7.1 ± 0.8 mm, SE) was about three times faster than at Bottle Run Point (2.4 ± 0.5 mm, SE) and about five times faster than at Middle Marsh (1.5 ± 0.6 mm SE). Clam siphon weights did not vary with patch size, nor did they vary among the three sites (Table 6c).

Seagrass shoot density, blade length, and species composition varied among sites

Table 4. Results from the four-factor ANOVAs on the shoot density, blade length, and % *Zostera* (arcsine transformed) from grass samples taken at the beginning and end of the experiment with large sized clams (mean size 41.9 mm). Date, energy and patch size are fixed independent variables and site (nested within energy regime) is random. Abbreviations as in Table 3.

		Density			Length			Zostera		
Source	DF	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Date	1	4226.76	10.02	0.10	1334.30	48.07	0.02	0.045	0.51	0.55
Energy	1	3094.01	2.36	0.26	144.80	1.54	0.34	3.779	0.59	0.52
Site(Energy)	2	2622.60	19.43	<0.01	188.26	10.80	<0.01	12.714	37.96	<0.01
Patch Size	2	784.75	5.81	<0.01	6.44	0.37	0.69	1.907	5.69	<0.01
Date*Energy	1	1020.51	2.42	0.26	101.89	3.67	0.19	0.548	6.13	0.13
Date*Site (Energy)	2	843.85	4.39	0.10	55.52	2.43	0.20	0.179	0.71	0.55
Date*Patch Size	2	900.08	4.68	0.10	3.24	0.14	0.87	0.761	3.00	0.16
Energy*Patch Size	2	539.08	4.18	0.10	68.99	2.12	0.23	0.577	0.98	0.45
Site(Energy)* Patch Size	4	257.83	0.95	0.44	65.00	1.86	0.13	1.175	1.75	0.15
Date*Energy* Patch Size	2	216.08	1.12	0.41	20.28	0.89	0.48	0.026	0.10	0.91
Date*Site(Energy)* Patch Size	4	384.33	1.42	0.23	45.77	1.31	0.27	0.507	0.76	0.56
Error	72	4860.25			627.62			12.056		

and between patch sizes in May and August samples (Table 7). Density generally increased from small to large patches at all sites on both dates, but the magnitude of the increase varied. Only at the Middle Marsh site in August did density show a decrease from small to large patches (Table 8). Blade lengths ranged from 9 to 19 cm and varied among sites and between patch sizes, but the effect was dependent on the date the samples were taken (Table 7, Table 8). The amount of *Zostera* generally decreased from small to large patches on both dates at all but the Middle Marsh site

Table 5. Mean density (shoots/m^2) and %*Zostera* by patch size and site averaged over replicate cores taken from small, medium, and large patches of seagrass at all four sites in August and December, 1990 (a), and the mean length of seagrass shoots by date and site (b). Numbers in parentheses represent ± one standard error. See Table 4 for ANOVA results.

	Patch size means ($n = 32$)			Site means ($n = 24$)			
(a) Grass data	Small	Medium	Large	Bottle Run Point	Middle Marsh	Cape Lookout	Oscar Shoal
density	2016 (332)	2918 (399)	2653 (265)	2374 (318)	1180 (132)	2507 (332)	4072 (464)
% *Zostera*	48 (8)	57 (7)	70 (6)	43 (8)	100 (0)	27 (4)	72 (5)

	Date means ($n = 48$)		Site means ($n = 24$)			
(b) Grass data	August	Decmeber	Bottle Run Point	Middle Marsh	Cape Lookout	Oscar Shoal
length	17 (1)	10 (0)	13 (1)	17 (1)	12 (1)	13 (1)

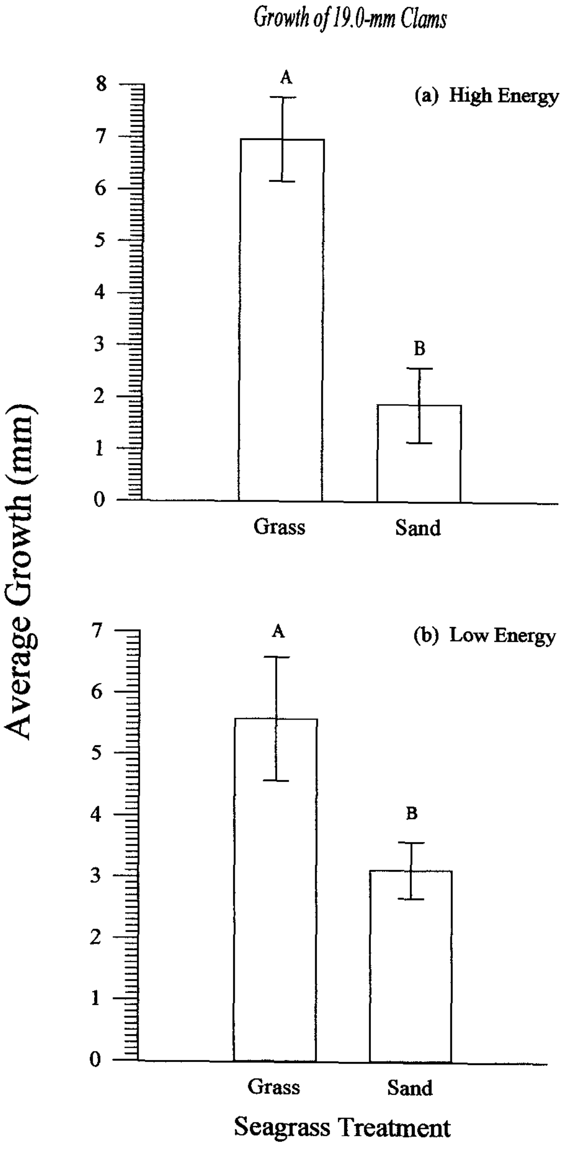

Figure 4. Average growth of small clams (19.0 mm) from vegetated and unvegetated sediments at high- (a) and low- (b) energy sites. Unlike letters denote treatments that differed from each other in Tukey *post hoc* comparisons and error bars represent ± one standard error. ANOVA results presented in Table 9b.

Table 6. Results from the two-factor ANOVAs on (a) the mean initial size of surviving clams, (b) mean growth of survivors, and (c) mean siphon weights (ANCOVA with mean body weight as the covariate) for small clams (mean size 22.3 mm) with site (fixed), and patch size (fixed) as the independent variables. Abbreviations as in Table 3.

(a) dependent variable: mean initial size

Source	DF	SS	*F*	*P*
Site	2	2.41	2.29	0.12
Patch Size	1	1.64	3.13	0.09
Site*Patch Size	2	0.55	0.52	0.60
Error	30	15.78		

(b) dependent variable: mean growth

Source	DF	SS	*F*	*P*
Site	2	222.48	84.09	<0.01
Patch Size	1	0.0007	0.00	0.98
Site*Patch Size	2	0.66	0.25	0.78
Error	30	39.69		

(c) dependent variable: mean siphon weight

Source	DF	SS × 10^{-2}	*F*	*P*
Site	2	7.29	1.51	0.23
Patch Size	1	1.61	0.67	0.42
Site*Patch Size	2	8.57	1.78	0.19
Mean Body Weight	1	4.57	1.90	0.18
Error	29			

Table 7. Results from the three-factor ANOVAs on the shoot density (square-root transformed to homogenize error variances), blade length (log transformed to homogenize error variances), and % *Zostera* (arcsine transformed) from grass samples taken at the beginning and end of the experiment with small-sized clams (mean size 22.3 mm). Date, site, and seagrass treatment are fixed independent variables. Abbreviations as in Table 3.

		Density			Length			Zostera		
Source	DF	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Date	1	23.77	26.46	<0.01	1.431	37.17	<0.01	2.424	133.67	<0.01
Site	2	130.75	72.77	<0.01	0.996	12.93	<0.01	16.442	453.39	<0.01
Patch Size	1	13.11	14.59	<0.01	0.429	11.13	<0.01	1.754	96.74	<0.01
Date* Site	2	23.50	13.08	<0.01	2.105	27.33	<0.01	1.685	46.47	<0.01
Date*Patch Size	1	0.19	0.21	<0.01	0.237	6.16	0.02	0.887	48.54	<0.01
Site*Patch Size	2	5.55	3.09	0.05	0.170	2.21	0.12	0.957	26.40	<0.01
Date*Site* Patch Size	2	1.47	0.82	0.45	0.106	1.38	0.26	0.467	12.89	<0.01
Error	60	53.90			2.311			1.088		

Table 8. Summary of seagrass characteristics from 6 replicate cores taken in May and August, 1991 from large and small seagrass patches used in the experiment to test the effect of seagrass patch size on growth of small-sized clams (22.3 mm). Density is expressed in shoots/m^2 and lengths are expressed in cm. Numbers in parentheses represent ± one standard error. See Table 7 for ANOVA results.

		May			Aug		
		Patch size			Patch size		
Site	Grass data	Small	Large	Site means ($n = 12$)	Small	Large	Site means ($n = 12$)
Bottle Run Point	density	1194 (132)	2410 (398)	1857 (265)	3210 (225)	5677 (729)	4443 (517)
	length	14 (0)	10 (1)	12 (1)	18 (1)	19 (1)	19 (1)
	% *Zostera*	100 (0)	36 (4)	68 (10)	21 (6)	8 (3)	14 (4)
Middle Marsh	density	1326 (199)	1724 (265)	1459 (132)	1353 (464)	1034 (132)	1194 (225)
	length	22 (3)	15 (1)	19 (2)	18 (2)	13 (1)	15 (1)
	% *Zostera*	100 (0)	100 (0)	100 (0)	100 (0)	100 (0)	100 (0)
Oscar Shoal	density	3581 (438)	4775 (968)	4164 (531)	5796 (623)	8886 (1366)	7334 (849)
	length	10 (0)	9 (1)	9 (0)	17 (1)	17 (1)	17 (1)
	% *Zostera*	67 (4)	13 (1)	40 (9)	11 (4)	6 (2)	9 (2)
Patch size means ($n = 18$)	density	2042 (305)	2918 (451)		3448 (504)	5199 (915)	
	length	15 (2)	11 (1)		17 (1)	17 (1)	
	% *Zostera*	89 (4)	50 (9)		44 (10)	38 (11)	

(Table 8). The significant effect of site on growth of clams was not correlated to differences in density (Pearson Correlation Coefficient = 0.97; $P = 0.15$), the amount of *Zostera* (Pearson Correlation Coefficient = 0.79; $P = 0.42$), or blade length (Pearson Correlation Coefficient = −94; $P = 0.22$) averaged over both dates.

d. Growth of small clams—Energy and grass cover effects. ANOVA confirmed that the mean initial size of clams did not vary among treatments (Table 9a). The ANOVA on growth of clams indicated a significant effect of seagrass cover, but that the effect was dependent on the hydrographic regime (Table 9b). Clams grew significantly more within the seagrass under both high- and low-energy conditions, but the magnitude of the effect was significantly more pronounced at high-energy sites than at low (significant Tukey *post hoc* comparisons, Figure 4a, b). There was no effect of hydrographic conditions or seagrass cover on clam siphon weights (Table 9c).

Shoot density, blade length, and species composition all varied among sites, but the effect was dependent on the date that the samples were taken (Table 10). Density of seagrass shoots increased at all sites from March to June, but the magnitude of the effect differed among sites (Table 11). Blade lengths either remained the same or increased from March to June at five of the six sites and decreased at one site (Middle Marsh) while the amount of *Zostera* decreased at five of the six sites and increased at one (Cape Lookout) (Table 11). The marginally significant difference in growth of clams among sites was positively correlated to density of seagrass (averaged over both dates—Pearson Correlation Coefficient = 0.81; $P = 0.05$), but was not related to the amount of *Zostera* (averaged over both dates—Pearson Correla-

Table 9. Results from the three-factor, blocked ANOVAs on (a) the mean initial size of surviving clams, (b) mean growth of survivors, and (c) mean siphon weights (ANCOVA with body weight as covariate) of small clams (mean length 19.0 mm) with presence or absence of seagrass cover (fixed—blocked by site), energy regime (fixed), and site (random—nested within energy regime) as the independent variables. Abbreviations as in Table 3.

(a) dependent variable: mean initial size

Source	DF	SS $\times 10^{-2}$	*F*	*P*
Energy	1	8.33	0.10	0.76
Site(Energy)	4	321.6	2.67	0.18
Grass Cover	1	8.33	0.28	0.63
Energy*Grass Cover	1	1.33	0.04	0.84
Error	4	120.3		

(b) dependent variable: mean growth

Source	DF	SS	*F*	*P*
Energy	1	0.013	0.00	0.95
Site(Energy)	4	12.28	5.65	0.06
Grass Cover	1	42.86	78.91	<0.01
Energy*Grass Cover	1	5.25	9.67	0.04
Error	4	2.17		

(c) dependent variable: mean siphon weight

Source	DF	SS $\times 10^{-3}$	*F*	*P*
Energy	1	5.84	0.46	0.54
Site(Energy)	4	51.15	1.11	0.49
Grass Cover	1	1.19	0.10	0.77
Energy*Grass Cover	1	45.63	0.08	0.80
Mean Body Weight	1	51.81	4.49	0.12
Error	3			

Table 10. Results from the three-factor ANOVAs on the shoot density, blade length, and % *Zostera* (arcsine transformed) from grass samples taken at the beginning and end of the experiment with small-sized clams (mean size 19.0 mm). Date and energy are fixed independent variables and site (nested within energy regime) is random. Abbreviations as in Table 3.

		Density			Length			*Zostera*		
Source	DF	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Date	1	2006.82	9.46	0.04	6535.44	1.08	0.36	1.077	3.331	0.14
Energy	1	487.35	2.13	0.22	5019.69	0.87	0.40	0.334	0.98	0.38
Site(Energy)	4	913.93	2.69	0.04	23205.81	15.28	<0.01	1.359	6.37	<0.01
Date*Energy	1	380.02	1.79	0.25	7752.07	1.28	0.32	0.093	0.29	0.62
Date*Site(Energy)	4	848.87	2.50	0.05	24244.75	15.96	<0.01	1.303	6.11	<0.01
Error	48	4071.20			18227.37			2.559		

Table 11. Mean shoot density (per m^2) and blade length (cm) of seagrass, and % *Zostera* from five replicate cores taken in March and June, 1992 from three high- and three low-energy sites used in the experiment to test the effect of presence of seagrass and energy regime on growth of small-sized clams (19.0 mm). Numbers in parentheses represent ± one standard error. See Table 10 for ANOVA results.

Site	Grass data	March site means ($n = 5$)	June site means ($n = 5$)
Bottle Run Point	density	2281 (424)	3743 (198)
	length	10 (0)	21 (2)
	% *Zostera*	92 (4)	79 (9)
Middle Marsh 1	density	2626 (385)	3316 (398)
	length	9 (1)	11 (1)
	% *Zostera*	65 (3)	34 (5)
Middle Marsh 2	density	3050 (451)	5013 (995)
	length	14 (1)	12 (1)
	% *Zostera*	79 (7)	35 (9)
Cape Lookout	density	3342 (127)	4430 (928)
	length	12 (1)	12 (1)
	% *Zostera*	43 (3)	66 (15)
Oscar Shoal 1	density	2997 (172)	4748 (345)
	length	12 (0)	13 (1)
	% *Zostera*	70 (1)	50 (8)
Oscar Shoal 2	density	1883 (371)	5650 (822)
	length	9 (1)	8 (0)
	% *Zostera*	70 (11)	15 (3)

tion Coefficient = −.70; $P = 0.12$) or blade length (averaged over both dates—Pearson Correlation Coefficient = −0.50; $P = 0.31$).

e. Sediment stability—Energy and grass cover effects. The two-way ANOVA performed on the arcsine-transformed proportion of the fine fraction indicated a significant energy effect ($F_{(1,28)} = 100.3$; $P = 0.0001$), a significant seagrass effect ($F_{(1,28)} = 6.0$; $P = 0.0209$), and a significant energy by seagrass interaction ($F_{(1,28)} = 10.4$; $P = 0.0031$). Vegetated sediments at high-energy sites contained significantly more fine material and less sand than the unvegetated sediments (72 ± 4%, SE vs. 61 ± 4%, SE, respectively) while there was no difference in the %fines between vegetated and unvegetated sediments at low-energy sites (87 ± 4%, SE vs. 88 ± 2%, SE, respectively—Tukey *post hoc* comparisons).

4. Discussion

Past investigations on the effect of seagrass cover on growth of clams have demonstrated a variety of responses (Kerswill, 1949; Peterson *et al.,* 1984; Peterson and Beal, 1989; Arnold *et al.,* 1991; Coen and Heck, 1991; Irlandi and Peterson, 1991). From these studies several factors have been suggested to be important in controlling growth of suspension feeders in seagrass beds, including food availability (Peterson *et al.,* 1984; Judge *et al.,* 1993) and predation disturbance (Coen and Heck, 1991; Irlandi and Peterson, 1991). The results from this study indicate that sediment stability provided by seagrass may also influence growth of clams within vegetated sediments, particularly at high-energy sites.

Although the three experiments presented here were done during different time periods thus confounding direct comparisons, previous investigations suggest that comparisons of the growth data between large- and small-sized clams are reasonable. Irlandi and Peterson (1991) performed growth experiments to test the effects of seagrass cover and position in a grass bed on growth of small clams (mean length <30.0 mm) during spring/summer (May–September) and in late summer/fall (August–December). In both of these experiments clams consistently grew significantly less from the unvegetated sediments. It is reasonable to assume that the pattern of small-clam growth observed during the spring in this study would have been the same if the experiments had been conducted August to December when the large-clam experiment was performed.

As predicted, assuming stability of surface sediments to be important, sedimentary disturbances acted more strongly on small clams that have shorter siphons and burrow less deeply than large clams (Peterson and Beal, 1989). Although both large and small clams grew faster from within the vegetation at both high- and low-energy sites, the magnitude of the effect was greater at high-energy sites only for small-sized clams. This matches the sediment data where more fine material present within the seagrass at high-energy sites suggested a more stable sedimentary environment than in the adjacent unvegetated sediments.

Growth patterns of the clams, however, cannot be explained solely by sediment stability. Other factors must have contributed to the high growth rates of large clams from inside seagrass beds and to the increased growth of small clams in vegetation at the protected sites where grain size analysis suggests similar sedimentary dynamics both within and outside of the vegetation. Differential between-habitat disturbance by predators may be a contributing factor (Irlandi and Peterson, 1991). The survivorship data from these experiments (see Irlandi, 1993) suggest that patterns in mortality due to predation on small-sized clams were similar to patterns in growth; i.e., in most cases growth of clams was low where predation rates were high. Growth of large clams, however, did not appear to be influenced by patterns in predation mortality. Although sub-lethal predation disturbance, or siphon nipping, has been invoked to explain decreased growth of bivalves (e.g., Peterson and Quammen, 1982; de Vlas, 1985; Coen and Heck, 1991; Irlandi and Peterson, 1991; Kamermans and Huitema, 1994) it did not appear to influence growth of large or small clams in this study. This finding is consistent with caging studies that demonstrate little or no effect of natural sources of siphon nipping on shell growth of *Mercenaria* (Irlandi and Mehlich, 1995).

Increased food abundance in seagrass beds may also contribute to increased growth of clams within vegetated sediments (Peterson *et al.,* 1984; Judge *et al.,* 1993). This would explain the faster growth rates for large and small clams in seagrass beds at both energy regimes. Food resources available to suspension feeders within seagrass beds may come from phytoplankton and/or epiphytic diatoms that are sloughed into the overlying water column. Changes in seagrass density, blade length, and species composition with patch size and energy may differentially influence current flow, surface area for attachment of epiphytic microalgae, and/or sediment stability (Fonseca *et al.,* 1982; Fonseca and Fisher, 1986; Irlandi and Peterson, 1991; Fonseca and Cahalan, 1992). All of these factors may interact to influence food quantity and quality within seagrass beds. Chlorophyll abundance was not measured during this study, but it is possible that the relative contribution of planktonic algae vs. suspended epiphytic algae may have varied among treatments to produce the patterns in growth observed here.

The results from this study demonstrate that seagrass cover in exposed and protected sites differentially stabilize sediments offering an additional explanation for the observed pattern of faster growth of small-sized clams inside seagrass beds, especially at high-energy exposed sites. Based on these results, and conclusions from previous studies, predation disturbance, food availability, and sediment stability all appear to play a role in controlling growth of clams within vegetated sediments, but the relative importance of these factors may differ among seagrass beds and may vary with size of the clam.

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